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Permafrost regime affects the nutritional status and productivity of larches in Central Siberia

Anatoly S. Prokushkin[1]*, Frank Hagedorn[2], Oleg S Pokrovsky[3], Jerome Viers[3], Alexander V. Kirdyanov[1], Oxana V. Masyagina[1], Marina P. Prokushkina[4], William H. McDowell[5]

[1,] V.N. Sukachev Institute of Forest SB RAS, Akademgorodok 50/28, Krasnoyarsk 660036, Russia, prokushkin@ksc.krasn.ru
[2] WSL, Zürcherstrasse 111, Birmensdorf 8903, Switzerland, frank.hagedorn@wsl.ch
[3] GET, Université Paul Sabatier-CNRS-IRD, 14 avenue Edouard Belin, 31400 Toulouse, France, oleg.pokrovsky@get.omp.eu
[4] Siberian Federal University, Svobodny 79, Krasnoyarsk 660041, Russia, mprokushkina@gmail.com
[5] University of New Hampshire, Department of Natural Resources and the Environment, Durham, NH 03824 USA, Bill.McDowell@unh.edu

* Correspondence: prokushkin@ksc.krasn.ru; Tel.: +791317825317

Abstract: Permafrost exerts strong controls on forest development through nutrient availability. The key questions of this study addressed the effect of site conditions on mass-based macroelement concentration and stable isotope ($\delta^{13}C$ and $\delta^{15}N$) dynamics during the growing season, and nutrient stoichiometry and resorption efficiency in foliage of two common larch species in Siberia. Foliar nutrient (N, P and K) concentrations of larches grown on permafrost soils were exceptionally high in juvenile needles as compared to those from a permafrost-free region, but were 2-fold lower with needle maturation. Within permafrost terrain trees from sites with a warmer and deeper soil active layer had 15-60% greater nutrient concentrations and higher $\delta^{15}N$ in their needles compared to shallower, colder soils. Larch of permafrost-free sites demonstrated enrichment of foliage in ^{15}N (+1.4 to +2.4 ‰) in comparison to permafrost terrain (-2.0 to -6.9 ‰). Seasonal dynamics of foliar d13C tended to decrease from June to August at all sites, positively correlating with mass-based N concentrations ($r=0.69$, $p<0.05$) and negatively with C:N ratio ($r=-0.79$, $p<0.05$). With senescence, nutrient concentrations in larch needles decreased significantly by 60-90%. This strong ability of larch to retain nutrients through resorption is the essential mechanism that maintains tree growth early in the growing season when soil remains frozen. High resorptive efficiency found for K and P for larches established on permafrost suggests nutrient limitation of tree growth within the Central Siberian Plateau not only by N, as previously reported, but also by P and K. Along with increased biomass (up to 50-fold), higher nutrient concentrations and ^{15}N enrichment of foliage in warmer sites indicate a strong response of larch stand productivity to a deepening of the soil active layer.

Keywords: permafrost, Siberian Larix spp., foliar nutrients, foliar $\delta^{13}C$ and $\delta^{15}N$, spatio-temporal variation, stoichiometry, nutrient resorption

1. Introduction

Absorption and storage of large amounts of atmospheric carbon (C) in the forest biomass and soil of the Northern hemisphere are among the central issues of the global greenhouse gas balance [1]. In this context, vast larch forests across Siberia may play an important role for carbon sequestration given the unique characteristics of *Larix* spp. [2] including its broad geographic distribution [3,4], the high photosynthetic capacity [5-7] and tendency to reach high stand biomass

under favourable conditions [2,8]. Mature larch stands across Siberia function nowadays as a relatively weak to medium sink of atmospheric CO_2 [9-11], and temperature, water and nutrient supply are known to be the most important abiotic variables controlling the sink strength under current conditions.

Although *Larix* species in continental Siberia are generally exposed to a water deficit [6,7,10], to offset the short growing period they typically show the highest photoassimilation rates among coniferous tree species when climatic conditions are favorable, not only on a yearly basis but also on a daily basis [6]. Such a strategy, nevertheless, is associated with greater water conductance, much higher transpiration water losses [6] and lower water use efficiency (WUE) for assimilated carbon [5]. This low WUE is particularly evident in the low values of $\delta^{13}C$ of foliage in comparison to co-occurring evergreen conifers [2,5]. There was a high spatial variability of larch foliar $\delta^{13}C$ among 20 locations in Northern hemisphere [5], as well as significant seasonal changes of foliar ^{13}C within a single site [9], indicating that environmental controls of larch foliar $\delta^{13}C$ and thus WUE still remain uncertain.

In conjunction with high photosynthetic rates, larch species of Northern hemisphere are characterized by the highest concentrations of nitrogen [2,5,9,12] and other macronutrients (e.g. P and K)[12] in foliage relative to evergreen conifers, very likely due to annually renewed needles. Thus, high nutrient demand to build foliar biomass may constrain the ability of larch taiga on permafrost soils to act as a sink of atmospheric C [13,14]. Globally, N and P are the most common nutrients limiting plant productivity and atmospheric C sequestration rates throughout terrestrial biomes [15-18]. In particular, N limitation is shown to be strongest in deciduous needle-leaf forests in high-latitude regions of the Northern Hemisphere due to slow N mineralization rates [13,18]. Nitrogen concentrations and natural isotopic abundance of N ($\delta^{15}N$:^{14}N) in plant foliage integrate ecosystem biogeochemical processes involved in N cycling and its sources within an ecosystem [19,20]. In particular, foliar $\delta^{15}N$ in boreal forest ecosystems is reported to respond positively to an overall increase of N availability in soils, as larger soil N "stimulates" loss of depleted N in soluble and gaseous forms and results in the $\delta^{15}N$ enrichment of the remaining pool. An important mechanism to offset nutrient limitation in plants in boreal biome is their symbiosis with fungi that is significantly changing the isotopic composition of N in host plant in comparison to bulk N source in soils [20]. *Larix* species are reported to rely on ectomycorrhyzal fungi [21] that are responsible for the most significant N depletion of host plant tissues [22]. All these factors might be of particular importance for permafrost terrains, where seasonal thawing of soil causes a gradual increase of soil depth (soil active layer) that is accessible for root exploration (e.g. decreasing dependence on fungal N) and, respectively, an uptake of isotopically distinct N early and late in the growing season (i.e. light N in topsoil vs. heavy N in subsoil) [23].

The resorption (retranslocation) of nutrients prior to leaf senescence is the main mechanism of nutrient preservation at the annual time scale [2,24-26], thus influencing whole tree survival on permafrost [27]. Indeed, nutrient retranslocation may supply a considerable part of the tree's nutrient requirements for new biomass production in the beginning of next growing season, when the soil remains frozen. N- and P-resorption efficiency, which is defined as the proportion of maximum nutrient pool resorbed prior to leaf abscission, ranges from 0 to 80% according to species and environmental conditions [25,26,28,] and is generally higher for *Larix* spp. in comparison to sympatric evergreen conifers and deciduous broadleaved [2].

Within permafrost-affected landscapes hydrology, thermal properties and biogeochemical processes of an ecosystem may strongly vary among specific sites. Sites with northern aspects receive lower insolation than those with southern aspects, resulting in cooler soils, slower thawing rates, and a shallower active layer. Poorly-drained habitats in depressions facilitate the development of forested peat bogs, which hampers mineralization of plant residues and in turn, induces lower soil temperatures due to higher soil insulation [29]. As a consequence, forest peatlands are nutrient poor as they primarily rely on atmospheric input of nutrients. Therefore, specific sites within the permafrost terrain may serve as a natural laboratory for analysing various aspects of nutrient cycling in forest ecosystems developed on cryosols.

The aim of this study was to estimate the effects of permafrost on the nutritional status of larch trees in Central Siberia and to assess possible responses of larch stands to projected warming at high latitudes. Our approach was to make use of a natural experimental set-up provided by the strong micrometeorological differences among sites within permafrost terrain: (i) Northern slopes with continuous permafrost zone; (ii) adjacent south-facing stands with deeper active layer, (iii) a fertile soil in the valley and (iv) a forested peatland and compared it with permafrost free sites further south. At these sites, we analysed the seasonal evolution of foliar concentrations of C, N, P, K and the and stable C and N isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of the main larch species (*Larix gmelinii* [Rupr.] Rupr and and *Larix sibirica* Ledeb). In our study, we address the following questions: 1) what are the temporal changes in foliar nutrient concentrations, stable isotope composition and nutrient stoichiometry throughout the growing season on permafrost and permafrost-free soils? 2) What are the primary nutrient limitations for *Larix* productivity at the leaf and stand scale across a gradient of permafrost regime and how does *Larix* cope with a low nutrient supply? 3) How do permafrost and its degradation likely affect nutrient availability and productivity of Siberian larch forests?

2. Materials and Methods

2.1. Study sites

Foliar nutrients of *Larix* spp. have been sampled in two regions of Central Siberia which differ in the extent of permafrost: the Tura site within the zone of continuous permafrost, and the Krasnoyarsk site in a permafrost-free area (Figure 1). Four tree stands of Gmelin's larch (*Larix gmelinii* [Rupr.] Rupr) were chosen near the Tura settlement in Central Siberia (64°19′ N, 100°15′E) to represent different sites: south-facing slope, north-facing slope, *Sphagnum* peatbog and stream valley (hereafter referred to as TS, TN, TB and TV, respectively) (Figure 1, insert). A detailed description of the plots was provided by Viers et al. [30] and given in Tables 1 and 2. Larch stands of all plots are developed on soils that originated from basalt parent rock, but range drastically in active layer thickness (Table 2). Importantly, three stands (TS, TN and TB) were regenerated after a ground fire in 1899. As a result of similarities in parent rock and fire history, the stand net carbon assimilation and nutrient cycling are thought to be controlled by intrinsic site-specific soil hydrothermal conditions.

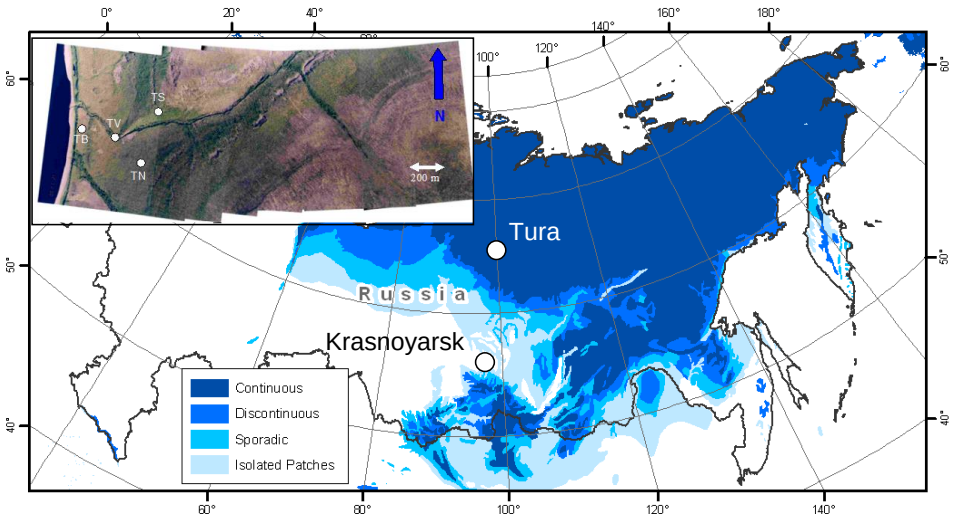

Figure 1. The map of Russia representing permafrost distribution (adapted from Brown *et al.* 1998) and location of study sites in Central Siberia. Inserted image shows location of plots in various habitats within permafrost site (Tura): TN – north-facing slope, TS – south-facing slope, TV – stream valley (riparian zone) and TB – *Sphagnum* peatbog.

Table 1. Plot and tree stand characteristics of the study sites in Central Siberia.

Stand dominant	Plot name	Latitude/longitude	Stand density, tree/ha	Age, yrs	Mean tree ring width, mm	DBH, cm	Tree height, m	Aboveground biomass, Mg/ha		
								trunk	needle	total
Krasnoyarsk: permafrost-free terrain										
L. gmelinii	L.g. KD	55°59′N 92°45′E	760	32	3.55±2.56	17.5	14.8	38.6	7.7	70.5
L. sibirica	L.s. KD	55°59′N 92°45′E	800	32	3.58±2.50	24.0	16.3	42.0	6.2	76.3
Tura: continuous permafrost terrain										
L. gmelinii	North-facing slope (TN)	64°19′21′′N 100°14′53′′E	4400	99	0.11±0.03	5.8	7.7	26.9	0.5	28.2
L. gmelinii	South-facing slope (TS)	64°19′32′′N 100°15′32′′E	2700	91	0.17±0.05	9.3	11.3	52.3	1.6	56.6
L. gmelinii	*Sphagnum* peatbog (TB)	64°19′30′′N 100°15′53′′E	2480	86	0.11±0.05	4.0	4.1	5.6	0.3	7.0
L. gmelinii	Riparian zone (TV)	64°19′29′′N 100°15′07′′E	1100	156	0.51±0.20	15.0	12.9	55.9	7.0	79.0

Table 2. Soil characteristics of plots selected in permafrost terrain. Data presented as mean (±SD).

Plot		Organic layer				Mineral soil				active layer thickness, cm^			$T_{5\ cm}$,&	rooting depth,
	Soil type*	OC,	$\delta^{13}C$	N,	$\delta^{15}N$	OC,	$\delta^{13}C$@	N,	$\delta^{15}N$@	June	July	August	Sept	
		kg/m²	‰	g/m²	‰	kg/m²	‰	g/m²	‰					oC	cm
Krasnoyarsk: permafrost-free terrain															
L.g. KD	Typic Haplocryalf	0.4	-	16	-	2.9	-	251	-	-	-	-	-	9.2	70
L.s.KD	Typic Haplocryalf	0.3	-	17	-	3.2	-	342	-	-	-	-	-	8.9	62
Tura: continuous permafrost terrain															
TN	Typic Aquiturbel	2.1	-28.35	54	-0.20	6.6	-27.12	307	3.24	1±1	25±12	36±11	42	2.8	12
TS	Typic Haplocryert	0.8	-29.04	22	-1.14	5.4	-27.47	309	3.43	18±8	86±15	112±26	123	6.6	64
TB	Sphagnic Fibristel	6.4	-28.64	96	0.19	5.5	-28.02	425	1.58	0	1±2	15±8	20	0.1	0
TV	Lithic Aquorthel	1.8	-29.67	60	-0.06	7.3	-28.21	365	2.31	5±2	52±16	63±19	88	4.1	45

*Keys to soil taxonomy (1998)

@Topsoil layer (0-10 cm)

^At the date of needle collection

&Mean summer (June-August) soil temperature at 5 cm depth for two consecutive years (2005-2006)

The climate in Tura is cold and dry with a mean annual air temperature of -9.1°C (1929-2012). Mean monthly air temperature varies from about -36°C in January to 16.5°C in July. Annual precipitation in this region is 371 mm, with 60-70% occurring during summer.

For comparison, *L. gmelinii* and *L. sibirica* stands were selected in adjacent plantations in the arboretum of the V.N. Sukachev Institute of Forest near Krasnoyarsk (Forest-steppe ecotone) (55°59'N 92°45'E). The mean annual air temperature in Krasnoyarsk is 0.9°C (1891-2009). Mean air temperature varies from about -16.8°C in January to 19.1°C in July. Mean annual precipitation is 500 mm (1967-2009). The soil is seasonally frozen (November-April). Ground vegetation is dominated by graminoids and a considerable portion of the area is covered with larch needle litter (for stand and soil characteristics, see Tables 1 and 2).

2.2. Sampling and analyses

2.2.1. Stand inventory and tree biomass measurements

In mid-August of 2006, we have established plots with 20 m long sides that served as the edge to define the start of a tree census. When counts within this 20 m border reached ca. 200 trees (adapted from the Russian standard for stand inventory), which also includes saplings (<1.3 m height) and dead trees, plot length was measured and total area was calculated. Taking into account different densities of trees, plot area varied among sites from roughly 200 to 1800 m^2. For every tree on the plot we have measured tree height, D0, DBH (the diameters at zero height and at breast height), crown length and assessed whether the tree was living or dead. Mean tree height and DBH were calculated for living trees in every stand. To estimate stand level total aboveground biomass and biomass of its fractions (trunk, branches and needles) we applied allometric equations based on model tree sampling. For this purpose, in every habitat from 7 to 10 trees from each diameter class (1-2 cm step) was logged and weighed for fresh biomass of trunk and crown (branches with needles) separately. Then subsamples of trunk (wood discs from D0, Ddbh, 2/3 and ¾ height), thick (>2 cm) and thin (< 2 cm) branches and needles from bottom, middle and top part of crown (3 mean branches) were sampled and dried in the oven at 105°C to obtain dry weight conversion coefficients for the respective fraction of aboveground biomass. Then plot-specific allometric equations were developed relating component biomass to diameter at breast height (DBH) and tree height (*h*) ($Y = \beta X\alpha$, where Y – biomass, X – DBH or h). The best fits for prediction of biomass were shown for diameter at breast height in all plots (R^2>0.93 for total and trunk biomass, R^2=0.58-0.83 for branches and needles). Further site- and fraction-specific allometric equations have been used for calculations of total aboveground biomass and fractions.

To obtain tree stand age and mean tree ring width (TRW), wood discs and cores of at least 20 trees have been analyzed in the laboratory by dendochronological methods [31]. Fire year (1899) has also been estimated dendrochronologically by dating fire scars of discs from 2-5 trees that survived the fire at every habitat.

2.2.2. Soils

Organic and mineral soil samples have been collected along the 10 m transect at the centre of each plot. The soil active layer depth (ALD) (annually thawed depth to permafrost) and surficial organic layer column (moss-lichen stratum and organic soil layer) have been measured by steel rod every 1 m (n=11). To measure stocks of organic layer we sampled 5 column replicates every 2 m. Collected material was separated into the live portion of ground vegetation and the organic soil layer (O). Subsamples of both portions were oven dried (105° C) to determine the ratio between moss-lichen stratum and organic soil layer, and bulk densities. Then the dependence between thickness and stock of organic layer column was used to calculate the mean transect-specific organic layer stock.

Sampling of mineral soil has been performed in soil pits beneath sampled organic layers (n=5) by 100 cm^3 cylinders with 3 replicates at every 10 cm depth for the entire active layer to permafrost table (20-120 cm). Rooting zone was determined as the maximum depth at which larch roots

appeared in soil pits. Under field conditions all fresh soils were sieved through a 2-mm mesh sieve with further removal of finer roots in the 2 mm fraction. In parallel, one cylinder sample has been collected to obtain soil bulk density by oven drying at 105°C in laboratory conditions. Then the 2 mm soil fraction and bulk organic layer samples were divided into subsamples which were used for C and N determination performed on finely ground samples (mixer mill, Retsch, Germany) and oven dried at 80°C (48 hours). Total mass-based concentrations of nitrogen and carbon were measured by Cu-O catalysed dry combustion at 900 °C with ≤0.5% precision for standard substances (Elementar Vario Maxi CHNS analyser, Elementar Analysensysteme GmbH, Hanau, Germany). Carbonate C was not detected in soils and all C in soils was recovered in organic form. The isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) were determined on soil samples (organic (O) layer and humic (A) horizons) collected in 2011 in the same sites using a Delta-S isotope ratio mass spectrometer (Finnigan MAT, Bremen, Germany) linked to elemental analyzer (EA-1108 Carlo Erba, Italy) via a variable open split interface (ConFlo-II; Finnigan MAT, Bremen, Germany). The $\delta^{13}C$ and $\delta^{15}N$ were determined in continuous flow mode. This guarantees a high sample throughput rate with good precision for $\delta^{13}C$ (r ± 0.1%) and $\delta^{15}N$ (r ± 0.2%). The isotopic values were expressed in the δ notation relative to the international standards:

$$\delta_{sample} = (R_{sample}/R_{standard} - 1) \times 1000;$$

where R_{sample} is the molar fraction of $^{13}C/^{12}C$, or $^{15}N/^{14}N$ ratio of the sample and $R_{standard}$ of the standards Vienna Pee Dee belemnite for C and atmospheric N_2 for N.

Values of total C and N were normalized to absolute dry mass of soil (after drying at 105° C). Further, bulk density of soil and respective C and N mass-based concentrations were used to calculate their stocks in layers of organic and mineral soil, which in the latter case was limited to 0.5 m for easier comparison among sites that varied greatly in active layer depth (20-120 cm).

2.2.3. Larch needles

Samples of larch needles were collected during the growing season of 2006, taking into account the differences in phenology between two sites located in northern and southern parts of the region, respectively. Sampling was carried out four times: started from juvenile needles on June 7 in Tura (60±4% of maximum mass and 73±6% of length attained in July) and May 25 in Krasnoyarsk (66±5% of maximum mass and 81±3% of length attained in August); continued with mature needles (July 18 and 21, respectively in Tura and Krasnoyarsk), then senescing needles (August 23 and 25) and ended at the coloured phase (yellow) just during needle shedding (September 12 and October 20). Samples of larch short shoot needles from 3-5 mid-crown branches were collected on every plot from three trees representing the mean tree of the stand (diameter at breast height and tree height) and similar live status (crown development).

After collection, the plant material was first cleaned on site with ultrapure water to remove surface particles, air dried and stored in clean plastic bags. Back in the laboratory, samples were dried at 80°C for 48 hours and finely ground using a mixer mill (Retsch, Germany). Total nitrogen and carbon mass-based concentrations and isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) in bulk samples of larch needles were measured by the same method as for the soil samples. As described earlier [30] for the analysis of phosphorus and potassium, samples were processed in a clean room (class A 10000). Between 100 and 200 mg of needle material was first digested in hydrogen peroxide (H_2O_2) for 24 hours at ambient temperature and further digested in HNO_3 + HF, for 36 hours at 80°C, then in HCl for 36 hours at 80°C, and finally, by HCl-HNO_3 treatment for 36 hours at 80°C. Measurements of P and K were conducted by ICP-MS (Agilent 7500 CE) using 3-point calibration against a standard solution of known concentration [30]. Indium and rhenium were used as internal standards to correct for instrumental drift and eventual matrix effects. The international geostandards Apple Leaves SRM 1515 (from NIST, USA), lichens BCR-CRM 482 (from BCR, Belgium), and Pine Needles SRM 1575a (from NIST, USA) were used to check the efficiency of both the acid digestion protocol

and the analysis. Data presented here are within 10% of deviation of recommended values for these international standards.

2.3. Statistical analyses

Results are shown as a mean of three replicates with standard deviation. Overall differences between sites in soil properties, stand and foliage biomass, foliar element concentrations, isotopic composition, stoichiometric ratios and resorption efficiencies were calculated using t-tests at $P<0.05$ level, which were performed among sites for Gmelin's larch in permafrost terrain and between both species under the same conditions in the arboretum at each sampling date. Linear regression analysis was performed to examine the relationships between soil site characteristics, foliar mass-based nutrient concentrations, isotopic composition and carbon isotope discrimination. The resorption efficiency was calculated as

$$\%RE = (N_{green} - N_{sen}) \times 100 / N_{green},$$

where N_{green} is the concentration of a nutrient in green needles collected before senescence in August, and N_{sen} is a nutrient concentration in senescent needles. All data treatments and statistical analyses were performed using STATISTICA ver. 6 (StatSoft Inc.).

3. Results

3.1. Tree and soil parameters

Permafrost and permafrost-free sites varied greatly in stand biomass (Table 1) taking into account the differences in the stand ages (>86 years vs. 32 years, respectively). Mean diameter, mean height and total biomass of the young larch stand in the permafrost-free site were comparable to 156-year old intrinsically nutrient-rich riparian zone (TV) in permafrost terrain. Greater productivity of larch species in permafrost-free environment is also evident from 7- to 32-fold higher mean tree ring width (TRW) for both *Larix* species in Krasnoyarsk in comparison to larch trees of permafrost-affected sites. In the permafrost terrain at Tura, larch stands of similar age demonstrated also high inter-habitat variation. Mean tree diameter (DBH), height and tree-ring width differed about three-fold between *Sphagnum* plot (TB) and riparian zone (TV, Table 1). Stands developed on the slopes (TN and TS plots) were intermediate among those extremes, and higher growth of larch trees was found for the south-facing slope. Aboveground stand biomass had even larger differences among sites (>10-fold), i.e. 7-79 Mg/ha for total biomass and 0.2-7.0 Mg/ha for foliar biomass and increased with active layer depths (Figure 2a).

Carbon and nitrogen stocks in the upper 0.5 m of soil in different sites ranged from 3.3 to 11.9 kg C/m^2 for total C and 0.3 to 0.5 kg N/m^2 for total N (Table 2), with a close positive correlation between C and N ($r=0.92$, $p<0.05$). The greatest values existed in permafrost terrain with the maximum amount of accumulated C and N in the soil of forested peat bog (TB, 11.9 kg C/m^2 and 0.5 kg N/m^2). The distribution of soil C and N between organic and mineral soil layers showed an increasing portion of organic layers with the severity of hydroclimatic conditions. In the in peat soil (TB site), the organic layer comprised more than 50% and 18% of the total C and N stocks.

Soil $\delta^{15}N$ increased with soil depth and differed significantly among sampled sites: from +0.2 to -1.2‰ in organic layers and +1.6 to +3.4‰ in A horizons. Soil $\delta^{13}C$ did not vary among sites, but increased slightly from organic layers (variation from -28.3 to -29.7‰) to the A horizons (-27.1 to -28.2‰).

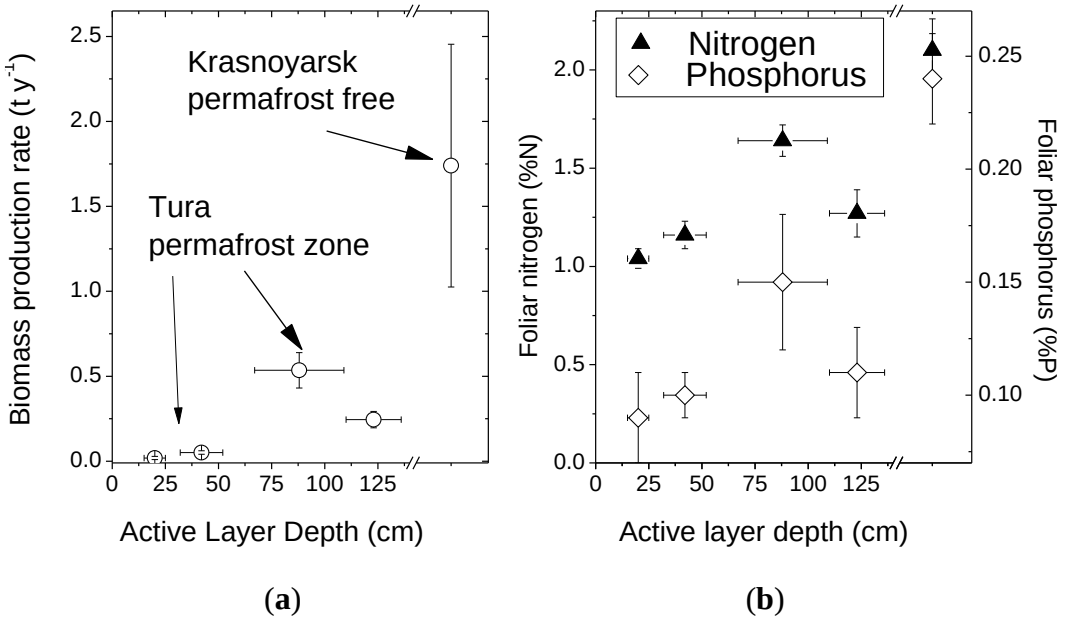

Figure 2. Stand-specific stem biomass production rates of *Larix gmelinii* trees (**a**) and foliar N and P concentrations in mature needles (August) in relation to respective soil active layer depth of the four sites of the permafrost terrain and permafrost-free site (**b**).

3.2. Seasonal dynamics of foliar element concentrations and stable isotope composition

Needles of larch species in both sites show relatively similar patterns in the seasonal course of C concentrations (Figure 3a) with a peak in August (46.7-48.7%) followed by lower concentrations prior to abscission. The annual net gain of C in foliage calculated for individual trees (based on allometric equations) ranged from 0.11±0.05 kg C/tree in the TB to 2.17±0.59 kg C/tree in the riparian zone (TV). At the stand level, assimilated C in foliar biomass varied from 0.15 in TB to 3.40 t C/ha in TV and reached 3.70 t C/ha in the permafrost-free terrain.

The $\delta^{13}C$ values of larch foliage had highest values in juvenile needles and decreased during the growing season in both permafrost and permafrost-free terrains, except for plot TV (Figure 3b). Maximum depletion in heavy isotope during the season was up to 2-2.4 ‰, which was characteristic for colder sites as TN and TB (ranged from -28.1 ‰ in June to -30.4 ‰ in September). To estimate leaf carbon isotopic discrimination (Δ_{leaf}), the surrogate for water use efficiency (WUEi) by the equation of Farquar et al. [32], we took mean -7.7 ‰ as the $\delta^{13}C$ value in atmospheric CO_2 obtained in the Zotino tall tower observatory (ZOTTO, 60 °N, 90°E) for June-August of 2008-2010 (SD = 0.3‰, range -8.5 to -7.1 ‰). Carbon isotopic discrimination in juvenile larch foliage showed little variation among permafrost habitats (21.2‰±0.4‰), but increased during the growing season by 1.5-2 ‰, as opposed to ca. 1.2 ‰ enrichment of atmospheric CO_2 throughout the growing season. In August, "colder" sites (TN and TB) had generally higher Δ_{leaf}: (23.3‰±0.2‰) as compared to "warm" sites TS and TV (22.0±0.4‰).

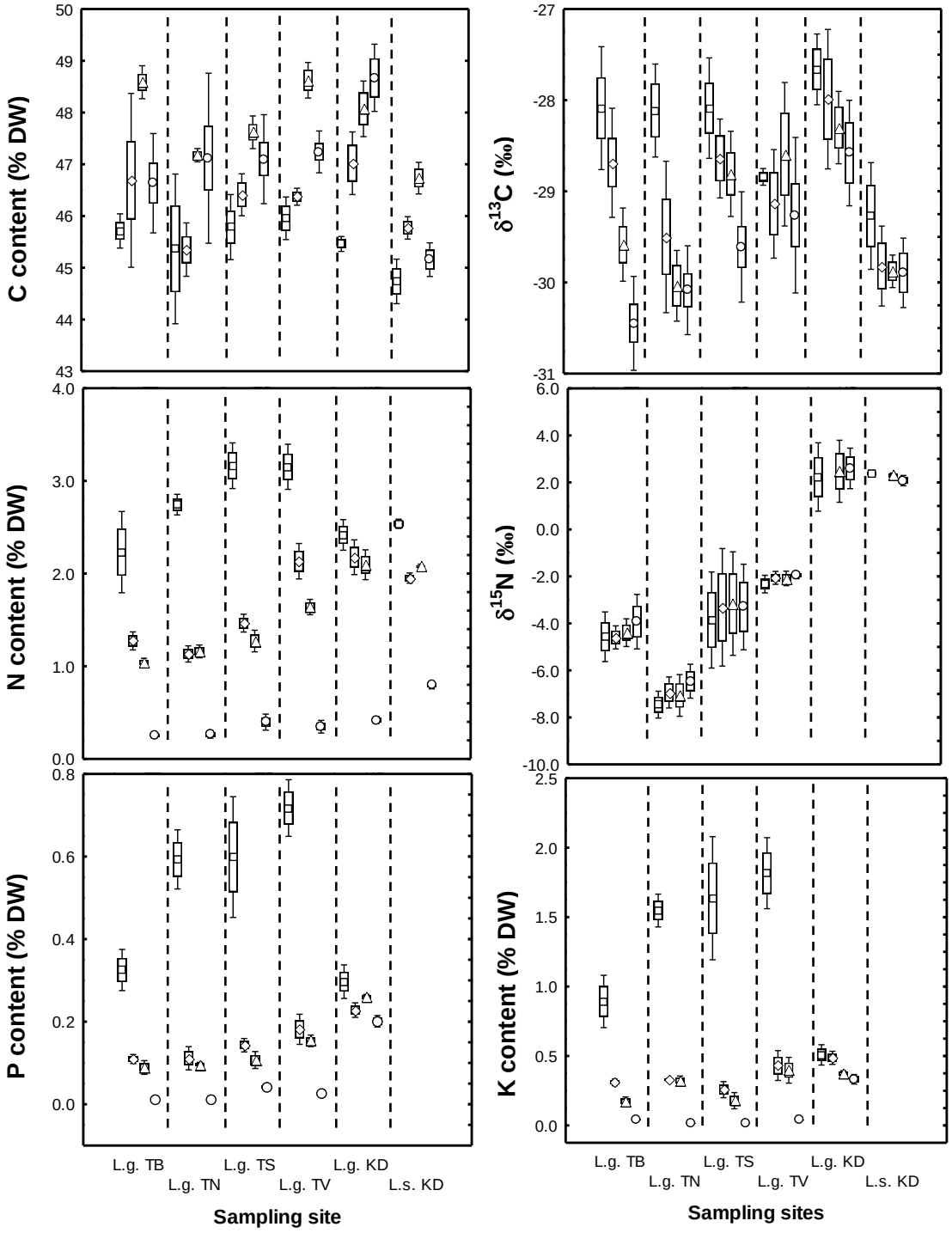

Figure 3. Seasonal evolution of mean contents of major elements (C, N, P and K) and stable isotope composition ($\delta^{13}C$, $\delta^{15}N$) in needles of two larch species (L.g. – *Larix gmelinii*, L.s. – *Larix sibirica*) from stands developed on continuous permafrost (Tura: TB – *Sphagnum* bog; TN – north-facing slope, TS – south-facing slope, TV – riparian zone) and from a permafrost-free site (Krasnoayrsk: KD). Means of 3 replicate trees for different dates of sampling following phenological differences in Tura and Krasnoyarsk, respectively: squares – 07.06.06 and 25.05.06, diamonds – 18.07.06 and 21.07.06, triangles – 23.08.06 and 25.08.06, circles – 12.09.06 and 20.10.06. Box: mean±SE; Whisker: mean±SD.

Mass-based macronutrient (N, P and K) concentrations of larch needles showed also a typical seasonal pattern (Figure 3c, e and f), which was more pronounced at the permafrost sites. Here,

nutrient concentrations in larch needles decreased by a factor of 2 to 9 from the early season until July and August ($p<0.01$). "Warmer" sites in the permafrost zone had generally higher early season macronutrient concentrations in needles (31±0.8 mg N/g, 6.0±1.5 mg P/g and 16.0±1.4 mg K/g d.w.) than larch trees growing in the *Sphagnum* bog (22±0.4 mg N/g, 3.3±0.5 mg P/g and 8.9±1.9 mg K/g d.w.)($p<0.01$). In comparison to the permafrost site, seasonal changes of nutrient contents at the permafrost-free soils (Krasnoyarsk) were negligible for P and K, and only a 10% reduction was observed for N. As a result, the mid-summer nutrient contents in needles of Tura larches on permafrost are around 50% lower than values found in trees growing on permafrost-free soils.

On a stand level N, P and K allocated in foliage of trees in permafrost-affected stands ranged drastically among sites and increased with active layer depth (Figure 2b). Largest pools of nutrients in foliar biomass were found in the permafrost-free terrain, following the order TB<TN<TS<TV<KD (Figure 4).

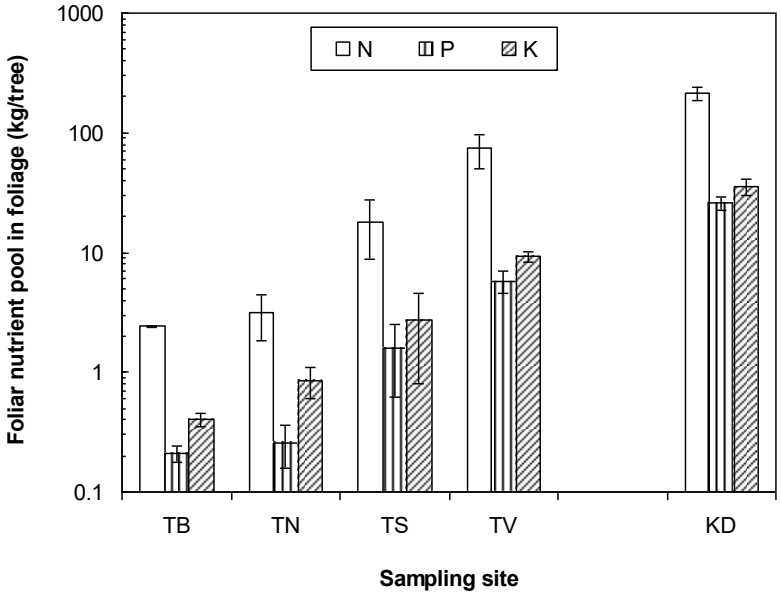

Figure 4. Nutrient pool/annual recruitment of major nutrients (N, P and K) in foliar biomass of Gmelin's larch in permafrost-affected (TB, TN, TS and TV) and permafrost-free sites (KD).

Foliar nitrogen stable isotope ratio ($\delta^{15}N$) showed only little temporal variation during growing season, but differed by as much as 9 ‰ among sites (Figure 3d). While the needles of permafrost-free site had positive $\delta^{15}N$ values of +2 ‰ in both *Larix* species, the north slope at Tura and the peat bog had values of -7.0 ‰ and -5.0 ‰, respectively.

The C-to-N, N-to-P and C:N:P ratios from permafrost habitats showed an opposite trend compared to mass-based concentrations of macronutrients. Elemental ratios were relatively narrow at the beginning of the growing season, though 2-fold higher C:N:P ratio was observed in needles of TB (Table 3). The C:N ratio ranged from ca. 15 in TS and TV to 18 and 22 in TN and TB, respectively ($p<0.01$). The N:P ratio of juvenile needles showed certain differentiation among sites ranging from 4.7 in TN site to 6.8 in the TB with intermediate values shown for TS and TV sites. In comparison to these values, Gmelin's larch from Krasnoyarsk showed, at the same development stage, an N:P ratio of 11 and C:N of 19. The N:P ratio increased during the growing season (up to 12.0±0.2 in August), and showed surprisingly low variation between the sites. *L. gmelinii* from the permafrost-free site showed an opposite trend, with N:P ratio decreasing from 11.1 (May) up to 8.3 (August). The C:N:P stoichiometric ratio changed significantly in mid-season for the compared sites. Within the permafrost region, needles from nutrient-poor and cold plots like TN and TB yielded generally larger C:N:P ratios compared with nutrient-rich sites. By contrast, at the Krasnoyarsk site, the C:N:P composition in Gmelin's larch foliage was more narrow (190:8:1), and reflecting a slight enrichment of nutrients in the mature foliage (Table 3).

Table 3. The dynamics of C:N:P ratio in foliage of *L. gmelinii* from different habitats in the permafrost region and the permafrost-free site.

	Permafrost-affected plots					Permafrost-free plot
Date of sampling	TB	TN	TS	TV	Date of sampling	L.g. KD
07.06.2006	144:6.8:1	77:4.7:1	78:5.4:1	71:4.8:1	31.05.2006	209:11.1:1
18.07.2006	440:11.7:1	421:10.5:1	327:10.3:1	293:13.4:1	20.07.2006	190:8.8:1
23.08.2006	557:11.9:1	493:12.1:1	451:12.0:1	335:11.3:1	25.08.2006	190:8.3:1
12.09.2006	4566:24.8:1	3227:18.0:1	1020:8.4:1	1236:8.9:1	20.10.2006	194:1.7:1

Senescing needles showed an abrupt reduction of mass-based nutrient concentrations in comparison to the preceding sampling in August, but demonstrated a positive correlation with green tissues ($r=0.97$ and 0.96 for N and P, respectively, $p<0.01$). Analysis of species-specific nutrient resorption revealed that needles of *L. gmelinii* exhibited higher retranslocation of N to stem/branches prior to senescence when compared with *L. sibirica* (80% vs. 62%, respectively, $p<0.05$) growing in the same plantation (Figure 5). The intra-species variation of resorption analyzed for *L. gmelinii*, growing in permafrost-free and permafrost sites, demonstrated relatively lower values in the latter case, ranging from 66% on the south-facing slope (TS site) to 79% in the riparian zone (TV). There was negligible resorption of P and K in senesced needles in foliage of *L. gmelinii* from the permafrost-free site. In contrast, when growing in permafrost-affected sites, this species showed significant ($p<0.01$) withdrawal of both P (53-88%) and K (74-95%). In particular, needles from the north-facing slope had the highest resorption efficiency for K (96%), while the highest resorption for P (88%) was found for the peatbog site. As an average for permafrost terrain, the order of increasing nutrient resorption was K>P>N (84, 76 and 75 %, respectively). On the spatial basis, mean nutrient resorption decreased in the order TN>TV>TB>TS (85, 82, 79 and 72%, respectively). As a result of resorption, larch lost with needle litter only 19-25% of its nitrogen, 12-47% of its P and 5-27% of its K.

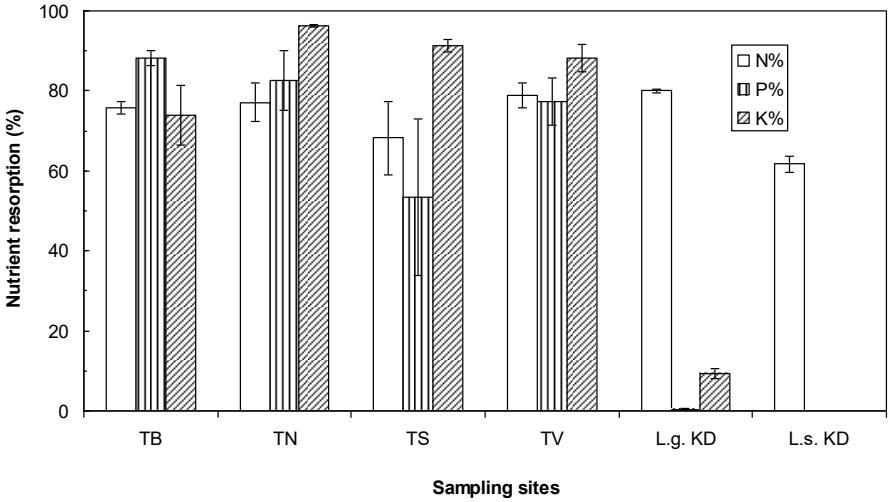

Figure 5. Mean intra- and inter-species variation of nutrient resorption efficiency of larch species from a permafrost-affected (Tura) and permafrost-free (Krasnoyarsk) sites. Resorption of P and K is not available for *L. sibirica* (L.s. KD) as these elemental concentrations were not measured in senesced needles.

4. Discussion

Our study along a gradient in permafrost regime in Central Siberia showed that (1) the nutritional status of larch trees reflected by the concentrations and pools of macro nutrients strongly

improved with the depth of the active layer which goes along with increased tree productivity. (2) In permafrost soils, we also observed a strong temporal dynamics in needle nutrients with a high resorption in autumn and a high nutrient investment into juvenile needles which might be a strategy of larch to become photosynthetically highly active despite frozen soils early in the season. (3) Finally, increasing needle $\delta^{15}N$ values with increasing active layer depth strongly suggests that cycling of N and possibly other nutrients will accelerate with permafrost melt which likely contributes to an increasing productivity of larch stands in Siberia.

4.1. Nutrient status of larch improves with active layer depth

The mass-based concentrations of major nutrients in needles of *Larix* spp. in mid-growing season observed in this study are in the lower range of reported values for Eurasia and Northern America [5,9,12,25](Figure 6). At the permafrost site at Tura, concentrations of N, P and K in mature needles were 50% less than the optimum contents of major nutrients in larch needles (2.1-2.6% for N, 0.3-0.6% for P and 0.9-2.0% for K) reported by [12]. Along the gradient in permafrost regime, the macronutrient concentrations in larch foliar biomass increased with increasing active layer depth reflecting improving site conditions (site fertility index or "bonitet" in Russian system). This increase was also reflected in a higher productivity of larches under favorable conditions, strongly suggesting that an improving nutrient availability contributes to the growth enhancement with increasing depth of the active layer.

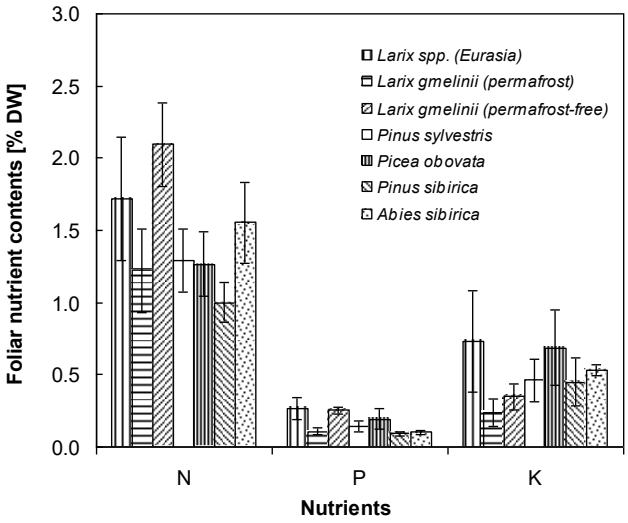

Figure 6. Mass-based concentrations of macronutrients in the foliage of main conifers of Siberia during the mid-growing season [12] compared with *L. gmelinii* collected at permafrost-affected and permafrost-free sites in this study.

Our data also suggest a threshold level of nutrient content in mature larch needles from this environment (ca. 1% for N), below which trees are likely to decline. On the other hand, larches from all permafrost-affected sites have a relatively narrow range of nutrient concentrations in foliage (e.g. 1.0-1.6% N) despite a 10-fold difference in overall standing stock and 25-fold difference of needle biomass between site with a shallow and a deep active layer depth. This pattern implies that an improving nutrient availability in the soil is rather reflected in aboveground biomass increment and in total nutrient uptake than in increased foliar nutrient concentrations. The gradient in nutrient availability among sites is probably also reflected in C allocation among below- and aboveground biomass. For our study region, Kajimoto et al. [33] reported that the poorly-drained and colder soils TB peatland site has 2-fold higher root-to-shoot ratio (1.13) in comparison to sites with larger active layer thickness (i.e. < 0.5). Such patterns are mainly explained by an increasing competition belowground for accessible resources within a limited soil volume.

Foliar stoichiometric ratios like N:P or C:N are reported as a good predictors of nutritional state of plants in nutrient-limiting environments [9,24]. At the plant level, N:P ratios of <14 and >16 corresponds to N- and P-limited biomass production, respectively, as demonstrated by fertilization experiments [16,24, 34]. However, the Eurasian data set for *Larix* needles by Girs [12] shows average N:P ratios of 6.5, which suggests a general N limitation of larch growth throughout Eurasia. In our study, N:P ratios increased from 4-6 in juvenile needles to 10 later in the growing season (Table 3), indicating that *Larix* is principally N limited but to a lesser extent than in other regions of Eurasia. The very small N:P ratio early in the season might not be indicative for a N limitation as N concentrations were very high with values of 3%. Interestingly, N-P ratios of the various sites within the permafrost region were very similar suggesting that they have similar physiological traits and/or adaptation to cold soils.

4.2. ^{15}N enrichment of needles on warmer soils

In larch stands of the studied permafrost region, N-pools varied from 0.2 to 1.0 Mg N/ha in the organic soil layers [35], and an additional 3.3-5.2 Mg N/ha (this study) or up to 6.6 Mg N/ha [36] in the mineral soil. Overall, the soil nitrogen pool usually exceeds 80% of the total ecosystem N pool in northern taiga [37]. Nevertheless, the availability of N and other nutrients for plants is limited due to small net N mineralization rates and plant growth largely depend on nutrient supply provided by ECM fungi. Hobbie and Högberg [38] reported that mycorrhizal fungi provided 61-86% of the N-uptake for arctic tundra plants and for Alaskan permafrost terrain and Mayor et al. [39] estimated that ECM-derived N may constitute 8-92% of black spruce annual demand. Our results showed that larches growing on deep active layers with smaller total soil N stocks had higher foliar mass-based N concentrations and elevated $\delta^{15}N$ values. The strong enrichment with ^{15}N in 'warmer' soils is indicative for an improved N supply [40, 20]. A soil warming study at the alpine treeline with *Larix* suggests that increased $\delta^{15}N$ values are related to increased contents of mineral N in the soil, which reduced the need to take up N via mycorrhiza which in turn induces ^{15}N depletion in foliar biomass [41]. Alternatively, ^{15}N enrichment may reflect N-uptake from the deeper unfrozen soils which are enriched in N as compared to the topsoil. The peat bog was an exception in this pattern with larches having higher foliar $\delta^{15}N$ values (ca. -5.0 ‰) in comparison to the north-facing slope. One reason could be a decreasing abundance of ECM fungi in bogs, because they are sensitive to waterlogging and P-limitation [42] and a consequence, larches in bog rely more strongly on mineral N. Except the peat bog, N concentrations and $\delta^{15}N$ values correlated positively with larch productivity, which strongly suggests that an improving N nutritional status with increasing depth of the active layer is an important driver for the better tree growth in warmer soils.

4.3. Strong seasonal dynamics in nutrient concentrations and ^{13}C

At the permafrost site, nutrient concentration showed a very strong seasonal variation with several fold decline throughout the growing season. The highest concentrations of foliar N, P and K at all permafrost-affected sites were found in the early growing season, when the needles were first produced. A similar pattern was reported for the same elements in Siberian larch from Mongolia [9] and micronutrients (i.e. Cu, B, Na, Ni etc.) in the same habitats for Gmelin's larch [30]. Elevated N, P and K concentrations are indicators of active metabolic processes and high photosynthetic rates (i.e. high Rubisco content) as well as high energy requirements and protein synthesis [43]. In our study, the initial peak in nutrient concentrations was much less pronounced at the warmer permafrost-free sites, suggesting that low temperatures are reinforcing this pattern. In support, Woods et al. [44] as well as Reich and Oleksyn [25] interpret the enrichment in foliar nutrients (mainly N and P) as an adaptation by plants to enhance metabolic activity and growth rates under low temperatures [25,44]. Remarkably, the highest concentrations of macro- and micronutrients in larch foliage of permafrost-affected sites occurred when the soil remained frozen and the uptake of nutrients from the soil was very limited. This indicates that the development of the photosynthetic apparatus in the early season is based on the large pool of nutrients accumulated during the previous growing season and stored throughout the winter. The substantial translocation of nutrients in larch needles from

year to year in permafrost terrains is supported by our findings of a strong resorption of nutrients in the permafrost sites but not on permafrost-free soils. Resorption is a key mechanism for deciduous plants to avoid losses of essential nutrients towards litter [24]. It is hypothesized to be particularly high at nutrient-poor sites [16] supplying a considerable proportion of a tree's nutrient requirement for new biomass production [24, 25]. The recycling of nutrients is even more essential for trees that renew their foliar on annual basis and which thus, require large quantities of C and nutrients to construct new photoassimilating biomass. Our results show that permafrost is even fostering nutrient resorption to support tree's life early in the following year.

We observed that juvenile needles were enriched in ^{13}C as compared to mature needles, which could indicate that storage carbohydrates (e.g. starch) that are generally more enriched in ^{13}C served as essential C source in early developmental stages [9]. However, also higher photosynthetic rates (and respective reduction of c_i/c_a ratio) under high foliar N and P levels may also lead to elevated ^{13}C in early season foliage of larch.

With the progression of the growing season bulk foliar ^{13}C decreased probably reflecting an increasing of proportion of current photoassimilates used for needle growth [9]. In addition, nutrient concentrations decreased strongly, which is typical for N in deciduous angiosperm species and evergreen conifers [12,45]. Much less marked changes are usually observed for foliar P and K, although some authors report their similar dynamics to N [46]. Likewise, nutrient concentrations in larch needles from the permafrost site changed predictably as a function of needle development and the needle C:N, C:P and C:K ratios increased significantly with needle maturation. Firstly, the foliar nutrients become diluted by increasing quantities of C-rich cell-wall material [26]. Higher lignification of needle tissues in nutrient-poor environments may further enrich needles in C-rich aromatic compounds [47], which might be indicated by the findings of lower $\delta^{13}C$ values in bulk needles as lignin is generally depleted in ^{13}C. Another reason reported for decrease of nutrients during a growing season is nutrient withdrawal to active growing zones (e.g. fine roots, shoots) and/or reproductive organs of plants growing on nutrient-limited soils [45,48].

5. Conclusions

Our results indicate that on permafrost soils, the preservation of macronutrients by resorption during autumn and the formation of juvenile needles with very high nutrient contents and particularly low N:P ratios at the beginning of the growing season is an important mechanism of larch trees to sustain a high metabolic activity early in the season, despite low air temperatures and frozen soils. Such a strategy may allow larch forests to cope with a low nutrient availability in cold soils in the short-term early in the season or even in the long-term for the entire life-span of trees where the development of thick soil-insulating organic layer induces a progressive nutrient limitation.

Our site comparison showed that with increasing active layer depth nutrient contents, $\delta^{15}N$ values and biomass productivity strongly increased. This pattern implies that deepening of soil active layer increases rates of nutrient cycling in soils which in turn stimulates the productivity of larch forests over vast permafrost regions of Siberia. Consequently, permafrost degradation by climatic warming may enhance the currently weak sink of atmospheric CO_2 in these landscapes (e.g. NEP = 76 $gC/m^2/a$ reported for Tura site [11]) if it is not outbalanced by increased CO_2 losses from soil organic matter which is so far locked in permafrost. An increased NEP can be expected as long as tree productivity is supported by an enhanced nutrient availability. Closely similar foliar N:P ratios observed in different sites of the permafrost region, contrasted with N:P ratio variation in permafrost-free sites, which suggests site-specific metabolic traits of Gmelin's larch and/or site-specific nutrient availability at local climatic and soil conditions. Along with site-specific resorption efficiency for these elements the observed patterns indicate that in permafrost terrains of the Central Siberian Plateau not only N, but also P and K may currently limit tree growth. Particularly, the higher efficacy of P and K resorption in poor and cold habitats reflects the plasticity of larches to maintain growth in severe environment.

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